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AND CLIPPING ON THE CHEMICAL
COMPOSITION OF *ANDROPOGON*
FURCATUS AND *STIPA SPARTEA*

A DISSERTATION SUBMITTED TO THE FACULTY OF THE
DIVISION OF THE BIOLOGICAL SCIENCES IN CANDIDACY
FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BOTANY
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By
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CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 572

ROBERT J. WEAVER

Introduction

The chemical composition of forage plants as influenced by season, habitat, and grazing has been studied by many investigators. Such studies supply information on the comparative nutritive value of plants at various stages of development, under varying environmental conditions, and under grazing. In investigations concerned with the improvement and maintenance of the forage cover, a knowledge of the nutritive value of the plants is just as important as their palatability, yield, and reaction to grazing. The chemical composition of tops of forage plants frequently grazed may be closely associated with the relatively small amounts of roots and tops usually produced by these plants.

There has been little investigation of the chemical composition of many of the grasses of the true prairie, especially in eastern Nebraska. Big bluestem (*Andropogon furcatus* Muhl.) and needle grass (*Stipa spartea* Trin.) were selected for this work, as they are dominants in the prairie, are valuable pasture grasses, and are found as chief constituents of the best native hay in eastern Nebraska. The purpose of this study was to compare the seasonal trend of the chemical constituents of these two species in two habitats and to note the effects of clipping on the composition of native and seedling plants.

Review of literature

GORDON and SAMPSON (8) and WATKINS (20) have extensively reviewed the literature concerning the chemical composition of range plants. Many investigators have found that in range plants there is a decline in the percentage of crude protein and minerals and an increase in the percentage of crude fiber from the earliest appearance of leaf blades to maturity (4, 8, 13).

The storage of sugars and starch in certain grasses was found to be inversely related to the growth rate, but hemicellulose showed a rather continued percentage increase throughout the growth cycle of the plants (14, 15, 17).

STODDART (19) concluded that season had a far greater influence upon chemical composition of *Symphoricarpos rotundifolius* than did either site or soil.

Soil type affects the chemical composition of plants in part through its effect on availability of nutrients and water (4, 5, 7). The soil type may also influence the species composition of the flora and thereby indirectly the chemical composition of the forage.

BROWN (3) used thermo-regulated growth chambers in his investigations and showed that temperature has a marked effect on chemical composition of grasses.

Forage that regenerates after grazing or clipping has been found to be very suc-

culent, with high percentages of crude protein and low percentages of crude fiber (11, 18).

Materials

Big bluestem, a sod-former, is the most important native tall grass in eastern Nebraska. Here this grass, although deeply rooted, is typically an indicator of moist but well-aerated lowland, but it also occurs in limited amounts and small size on the dry uplands. It is of southern derivation and normally resumes growth at Lincoln about April 15. Its vegetative growth is normally complete by September, after which seed is usually produced in abundance.

Needle grass is found characteristically on dry uplands and, if elsewhere, on lighter types of soil. It produces bunches usually 2-4 inches in diameter, and the root system varies usually from 3 to 5 feet in depth. It is of northern extraction and usually renews growth in eastern Nebraska early in March and flowers and produces seeds in late May or early June. It does not grow vigorously thereafter until the cooler weather of early fall but continues growth until winter.

Two stations were selected in virgin prairie about 3 miles northwest of Lincoln, Nebraska. One station was on moderately low, gently sloping land, and the other area was about $\frac{1}{4}$ mile distant on a hill-crest. The soil at the lowland station was Wabash silt loam; that at the upland station, approximately 30 feet higher, was Carrington clay loam. Topsoil on the upland was about 2 feet in depth and on the lowland about 3 feet deep. In the lowland there was an abundance of big bluestem and a small area where needle grass was dominant; the upland had large amounts of needle grass but only small bunches of big bluestem, scattered sparingly throughout.

Samples were taken throughout the growing season from the native grass at both stations, from areas on the lowland, which were repeatedly clipped at a height of 2 inches to simulate grazing, and from seedlings at both stations. The seedlings were grown in square-meter areas. In order to insure prompt, uniform germination and vigorous growth, the sod had been loosened to a depth of 2 inches, the coarser roots and rhizomes removed, and the soil well firmed, watered, and mulched after the seed had been planted.

Conditions for growth

The growing season of 1941 was characterized at Lincoln by a late spring, a wet April, moderate rainfall in May and June, and severe drought during July and August. Precipitation for April, May, and June was 3.12, 2.47, and 3.41 inches, respectively, or +0.59, -1.61, and -0.91 inches compared with the normal. The normal rainfall for July and August is 3.85 and 3.57 inches, but only 0.59 and 0.80 inches, respectively, fell during these months.

The mean monthly temperatures, April-August inclusive, are 54°2, 68°4, 72°6, 78°8, and 78°5 F., respectively. Temperatures were all above normal during 1941, excess temperatures being +2°7, +6°7, +1°2, +2°3, and +4°1 for the several months, respectively.

Evaporation from an open tank operated by the Weather Bureau at Lincoln was 7.1 inches in both May and June, 10.9 inches in July, and 10.2 inches in August.

Water content of soil, based on the total amount of moisture minus the hygroscopic coefficient at the various depths at each sampling, is shown in table 1. Several years of drought had preceded 1941; and, on March 31, soil on the upland was moist to a depth of only

29-39 inches and on the lower area to a depth of 49-57 inches.

On the upland, water was available for growth until late in June, after which very little occurred at any depth. Rain-fall of 1 inch on June 27 was the last shower in excess of 0.2 inch until August 23, when 0.49 inch fell. Available water content at the lowland station was greater at all times and at all depths than on

growth cycle and seeded abundantly. On the upland, water was applied only occasionally, and the big bluestem failed to produce flower stalks. Needle grass, however, produced seed in June. The showers, even in May and June, were poorly distributed for growth of seedlings. Therefore, the seedlings were watered as required to make possible adequate growth. An understanding of the devel-

TABLE 1
WATER CONTENT OF SOIL IN EXCESS OF THE HYGROSCOPIC COEFFICIENT
AT LINCOLN, NEBRASKA, DURING 1941

Depth in feet	Hygroscopic coefficient	March 31	May 10	May 24	June 20	July 11	July 24	Aug. 7	Aug. 31
Upland Station									
0-0.5.....	8.4	18.8	15.3	14.0	4.1	-1.2	-2.7	-0.9	-1.8
0.5-1.....	9.6	12.3	11.3	8.3	5.1	-0.3	-1.3	-1.1	0.6
1-2.....	11.0	9.8	10.8	12.1	6.0	0.6	0.0	-1.1	-0.5
2-3.....	10.0	4.2	8.0	8.6	5.5	0.3	1.8	-0.9	0.6
3-4.....	7.5	4.2		7.9	3.9	1.7	3.7	0.9	3.6
Lowland Station									
0-0.5.....	9.4	28.2	24.5	21.1	10.6	1.0	3.2	1.7	0.8
0.5-1.....	10.6	18.0	17.8	16.5	11.8	1.2	0.2	1.2	0.7
1-2.....	12.0	10.2	15.0	13.2	9.9	2.1	1.4	0.5	0.2
2-3.....	12.4	8.7	13.5	12.4	10.0	4.9	6.3	1.0	0.3
3-4.....	12.3	7.5		10.1	9.2	5.1	4.8	2.7	1.1
4-5.....	12.4	4.6		6.2			0.0	3.6	2.5

the upland. It, too, decreased sharply late in June, but water remained available, although often in small amounts, until August 31. These samplings for soil-moisture determinations were made near, but not in, the areas reserved for collecting plant materials. During the dry weather the area in the lowland from which the samples were taken for chemical analysis was supplied with enough water by sprinkling so that the grasses were able to continue growth. Those on the low ground completed their regular

opment of the grass at each station at the times of sampling is essential to an interpretation of the chemical composition.

Growth of the grass

BIG BLUESTEM

Development of big bluestem during the period of growth is shown by the data in table 2. The number of leaves was less on upland plants than on lowland after June 20 because of the extreme drought on the upland. There were green leaves on the watered lowland plants at

all times, but upland plants began to turn yellow or brown by July 10, and the leaf-tips dried despite watering. Actual decrease in general level of foliage of upland plants was also a drought effect; by August 7 the ends of the leaves had died back 2-5 inches and some whole shoots had died.¹ The plants were about one-third dried and had a dull-green color. Height of plants on lowland after July 10 was that of flower stalks; the general foliage level reached a maximum of about 26 inches. Plants on the upland produced no

the summer, but grass from the first clipping (May 13) was discarded, since it was the same as that of other lowland plants collected at this time. Material for the first analysis under this treatment was secured on June 5, when there were three or four leaf blades per shoot, projecting above the 2-inch-high clipping level, and the general height of the blades was 13 inches. By June 20 the plants had made an excellent recovery; most stems had two leaf blades above the clipping level, with a general height of

TABLE 2

GENERAL FOLIAGE HEIGHTS, NUMBER OF LEAVES, AND STEM DIAMETERS OF BIG BLUE-STEM ON LOWLAND AND ON UPLAND AT TIMES OF COLLECTION OF SAMPLES

DATE	LOWLAND			UPLAND		
	General foliage height (inches)	Average no. of leaves per culm	Range of stem diameter (mm.)	General foliage height (inches)	Average no. of leaves per culm	Range of stem diameter (mm.)
May 13.....	7	3		6	3	
June 5.....	18	5	3-4	10	5	2-3
June 20.....	20	5	2-5	16	5	2-3
July 10.....	22	6	3-6	14	5	2-3
Aug. 7.....	32	6	3-6	14	5	2-3
Sept. 1.....	40	6	3-6	11	5	2-3

flower stalks, and by September 1 more than half of their leaves and stems were dead, and only a few of the green leaves were turgid. On August 7 and September 1 in the lowland, the flower stalks, each with five small leaves, were collected separately from the unelongated shoots in the same sods.

CLIPPED BLUESTEM ON THE LOWLAND

Certain patches of big bluestem on the lowland were clipped six times during

¹ All height measurements reported in this paper, unless otherwise specified, are the general heights of the foliage or flower stalks in their natural condition; leaves were never straightened out in order to obtain a measurement.

10 inches. At the clipping on July 10, the foliage height was about 12 inches, and there were usually four leaves more than 2 inches high on each culm. Since some terminal growing-points did not renew growth after the earlier clippings, the stand of grass was thinned but growing vigorously. At the fifth clipping on August 7, the sturdy stems of the still thinner stand usually had five leaves which had an average height of 10 inches. On September 1, much growth of basal tillers had occurred, and there were four broad leaves per stem and an average height of 7 inches. This grass rapidly regenerates after close cutting or grazing (21).

BLUESTEM SEEDLINGS

Seed was planted on April 26 at both stations. By June 20, when the plants were first clipped, the average foliage height on the lowland was 4.5 inches. There was an average of twenty-five seedlings per square decimeter, and the plants were in the sixth-leaf stage. Many seedlings had one or two tillers, but the latter were too short to be included in the samples, which were clipped at a height of 1.5 inches. On the upland the average plant height was an inch less than for lowland plants, and there were only fifteen plants per square decimeter. The number of leaves and degree of tillering, however, was about the same as for plants on the lowland. On July 24 there was a thick stand of much-tillered plants on the lowland. They had been watered weekly and were thriving. The seedlings had about six leaves and were once more 4.5 inches tall. Those on the upland were only 3.5 inches high, and some plants were much dwarfed, despite similar weekly watering. A third clipping was secured on September 1 from the seedlings on the lowland. The seedlings were then vigorously growing; their average height was 6 inches, and nearly all had either five or six leaves each.

NEEDLE GRASS

Samples of *S. spartea* were collected seven times, April 23–September 1, inclusive. Foliage height was approximately the same at both stations at each sampling. On April 23, the general level of foliage was 5.5 inches, and the plants were in the third-leaf stage. By May 15 the general level of foliage was 13 inches, and the stems had an average of five leaves each. Inflorescences were present on some stems, but they were still enclosed in the leaf-sheaths. On June 5, flower stalks, which were harvested sepa-

ately, were 36–48 inches tall when held erect. Each had three short leaves above the 2-inch cutting height; these were left on the stalks. The seeds were in the dough stage. The general level of foliage was 18 inches high, and each unelongated culm had three or four long, tapering leaves. No further increase in general level of foliage occurred. On June 20 the fruits had all been shed, and the flower stalks, which were dead and dry at least throughout their upper half, were not included in this or subsequent samples. On July 11, plants on the lowland were green and thriving; on the upland the leaves were rolled tightly because of drought. At the sampling on August 7, one-third of the leaves on lowland plants were dry or nearly dry, a usual midsummer phenomenon, and on the upland nearly one-half of the foliage was bleached white and dried. At the last sampling—September 1—the late-summer, half-dried condition prevailed on the lowland; on the upland many bunches were entirely dry, but others were one-third green.

CLIPPED NEEDLE GRASS

By May 13, twenty days after the first clipping, the plants had made much recovery. The general level of foliage was 11 inches, and there were a few flower stalks in an early stage of development. The general level of foliage was again 11 inches on June 5. Each stem usually had two narrow leaves projecting above the clipping level. Since the plants were suffering from too frequent removal of the foliage, the third sample was not taken until July 11. Each stem now had three leaves previously unclipped, with a general foliage level of 14 inches. Some bunches contained very few stems, while others were one-third filled. By August 7, little regeneration of the clipped grass

had occurred. Only ten to twenty-five stems scattered throughout the large bunches renewed growth. The general height of foliage was about 7 inches, and each culm had an average of three to five leaves each. On September 1 the general level of foliage was 6 inches, and there were three leaves or parts of leaves per stem.

SEEDLING NEEDLE GRASS

The needle grass, planted April 26, grew more rapidly in the warmer and drier upland soil, where it had attained a general level of foliage of 7 inches when clipped on June 20. Seedlings were then in the third- or fourth-leaf stage. Most plants had one or two tillers, 1.5-2.5 inches in height. The stand was open, only about 8 plants occurring per square decimeter. When the needle grass on the lowland was clipped on July 3, it had attained approximately the same size and density of stand as that described on the upland. Needle grass on the upland regenerated to such a small degree that it was not clipped again. The grass on the lowland was harvested on September 1, when the plants had a foliage level of 5 inches and an average of three leaves per culm.

Methods

COLLECTION OF SAMPLES

Each composite sample for chemical analysis consisted of plants taken in at least five different places in the local experimental area. Further samples were never taken from the same place, thus assuring the natural growth and maturing of the tissues included in each sample.

In the clipping experiments, parts of many plants were included, as an area of about 1 square meter was clipped on each collecting date. The seedlings likewise

were all clipped at each of the several times of collecting, whether or not all material was used for the chemical analysis.

Samples were taken between 10:00 and 11:00 A.M. and in a definite sequence. They included the entire aerial portion of the plant, unless otherwise specified. The grass was placed in paper bags and taken at once to the laboratory, where it was then killed by being subjected to a temperature of approximately 100° C. It was placed on a 2-mm. mesh screen, and heat was applied from below by an electric heater with a large reflector. This arrangement permitted constant movement of large amounts of hot dry air. After 5-8 minutes the temperature was decreased to 70° C. for 15 minutes, and the final drying was in an electric oven at that temperature.

CHEMICAL ANALYSIS

When completely dry, the grass was finely ground and placed in tightly stoppered bottles. Duplicate samples were used for the determinations, and the analytical methods used were those described by LOOMIS and SHULL (12). The reduced-iron method adapted by PUCHER was used for determination of total soluble nitrogen.

Results

BIG BLUESTEM

It is emphasized that all analytical data in this investigation are expressed as percentage values and not as absolute amounts.

On each sampling date throughout the season, established plants on the lowland had the highest percentage of total sugars, clipped plants on the lowland the lowest, and upland plants had an intermediate percentage (table 3). Seedlings

on the upland contained about the same percentage of sugar as established upland plants, but the percentage sugar content of lowland seedlings was small.

Established plants on the upland contained the highest percentage of starch

of seedling plants in the two habitats was about equal.

The percentage sugar-starch content of established lowland grass was less than that on the upland early in the season, but it was greater on the lowland after the latter part of June, when drought be-

TABLE 3

PARTIAL CHEMICAL ANALYSIS OF ABOVE-GROUND PARTS OF BIG BLUESTEM AT SIX STAGES OF DEVELOPMENT, EXPRESSED AS PERCENTAGES OF OVEN-DRY WEIGHT

Plants	Date collected	Total sugars	Starch	Total sugars and starch	Hemi-cellulose	Soluble nitrogen	"True" protein	Total ash
Upland.....	{ May 13	1.7	6.8	8.5	13.8	0.30	12.5	8.5
	{ June 5	2.9	6.4	9.3	18.5	.17	7.7	5.3
	{ June 20	1.4	6.5	7.9	17.6	.16	6.1	5.5
	{ July 10	3.4	3.9	7.3	21.6	.12	4.8	5.2
	{ Aug. 7	1.8	3.7	5.5	21.4	.10	3.2	4.5
	{ Sept. 1	1.0	3.8	4.8	20.6	.09	2.6	5.1
Lowland.....	{ May 13	1.9	4.6	6.5	13.2	.41	15.0	9.5
	{ June 5	3.2	4.1	7.3	19.5	.14	7.8	6.4
	{ June 20	1.9	5.8	7.7	20.3	.13	5.6	6.2
	{ July 10	4.5	4.1	8.6	21.6	.11	4.2	5.9
	{ Aug. 7	3.1	3.4	6.5	22.8	.09	3.2	5.4
	{ Aug. 7*	4.0	3.9	7.9	23.5	.09	2.4	4.3
	{ Aug. 7†	1.9	2.6	4.5	21.8	.10	4.5	7.1
	{ Sept. 1	2.0	4.7	6.7	23.8	.08	2.5	5.7
	{ Sept. 1*	2.1	4.8	6.9	24.2	.07	2.2	4.7
Lowland, clipped....	{ May 13	1.9	4.6	6.5	13.2	.41	15.0	9.5
	{ June 5	2.3	3.8	6.1	15.9	.16	9.5	8.0
	{ June 20	0.8	3.9	4.7	13.7	.27	11.6	9.7
	{ July 10	1.6	2.0	3.6	18.9	.16	8.3	7.7
	{ Aug. 7	1.6	1.8	3.4	18.7	.14	7.3	7.2
	{ Sept. 1	0.9	4.0	4.9	18.5	.14	7.1	7.6
Upland seedlings....	{ June 20	1.6	4.9	6.5	12.0	.16	10.1	7.1
	{ July 24	3.0	3.8	6.8	15.5	.18	7.2	6.0
Lowland seedlings...	{ June 20	0.9	4.5	5.4	12.7	.19	8.3	8.4
	{ July 24	2.0	3.7	5.7	18.6	.16	7.2	7.7
	{ Sept. 1	1.5	3.2	4.7	15.5	0.13	7.1	8.2

* Analysis of stems and flowers.

† Analysis of leaves.

(about 6.5 per cent) at the first three sampling dates (table 3). Clipped plants on the lowland contained the lowest percentage of starch except at the September 1 collection, when they approximately equaled the upland plants in percentage starch content. The starch content

came severe on the upland (fig. 1). Upland seedlings had a higher percentage content of this fraction than did those growing on the lowland. The lowland clipped plants had a gradually decreasing sugar-starch fraction during most of the season.

The percentage of hemicellulose increased generally during the growth cycle of the plants (fig. 1). Established plants on the lowland usually contained a higher percentage of hemicellulose than the corresponding upland plants. The percentage content of this fraction in seedlings at the time of sampling was less than in established plants growing near by. The clippings from established grass at the lowland station contained a smaller percentage of hemicellulose than did the unclipped plants.

On May 13, established lowland plants contained more total soluble nitrogen than did corresponding upland plants; but, after June 5, upland plants had a higher percentage of their weight in this fraction, although after June 20 the difference was probably not significant (fig. 1). Seedling plants had, in general, a higher percentage of soluble nitrogen than did the established plants. Clipped plants on the lowland, with one exception, had a higher percentage of soluble nitrogen than did unclipped plants.

The graph showing percentage changes of "true" protein is, in general, similar to the graph for total soluble nitrogen (fig. 1).

Established plants had a relatively high percentage of ash at the first sampling (fig. 1). Lowland plants had consistently about 0.5-1.0 per cent higher total ash content than did upland plants. Seedlings had a higher percentage ash content than the corresponding established plants did, and established plants on the lowland, which were clipped throughout the season, maintained a high percentage level of total ash.

The chemical composition of flower stalks and leaves at the last two sampling dates is shown in table 3. On August 7 each inflorescence was about one-half exerted, and by September 1 they were

partly to fully expanded. On August 7 the flower stalks contained almost twice the percentage of sugar and starch as did the leaves, but by September 1 the percentages were approximately equal. There was slightly more hemicellulose on a percentage basis in stalks than in the leaves. On August 7 the ratio of percentage of "true" protein in flower stalks to percentage in the leaves was about 1:1.9, but by September 1 this ratio had been reduced to 1:1.4. Leaves contained about 1.6 times as much total ash as did the flower stalks on a percentage basis.

NEEDLE GRASS

The percentage content of total sugars was relatively high early in the season (table 4), and established plants on the upland usually had the highest percentage content of total sugars. These data indicate that the percentages of starch and of sugar plus starch decreased as the season advanced and that no one treatment had the highest percentages of these compounds at all samplings (fig. 2).

Established plants on the upland contained a higher percentage of hemicellulose than did the corresponding lowland plants (fig. 2). Clippings from established and seedling grass usually contained smaller percentages of hemicellulose than did unclipped plants.

Graphs showing percentage changes of total soluble nitrogen and "true" protein in the grass are, in general, similar (fig. 2). The percentage content of these constituents decreased with the advancing season, and all clipped plants had a higher percentage of their weight in these fractions than did unclipped plants.

Established plants on the lowland maintained a higher percentage ash content than did either established plants on the upland or clipped established plants on the lowland (fig. 2). Clipped seedlings

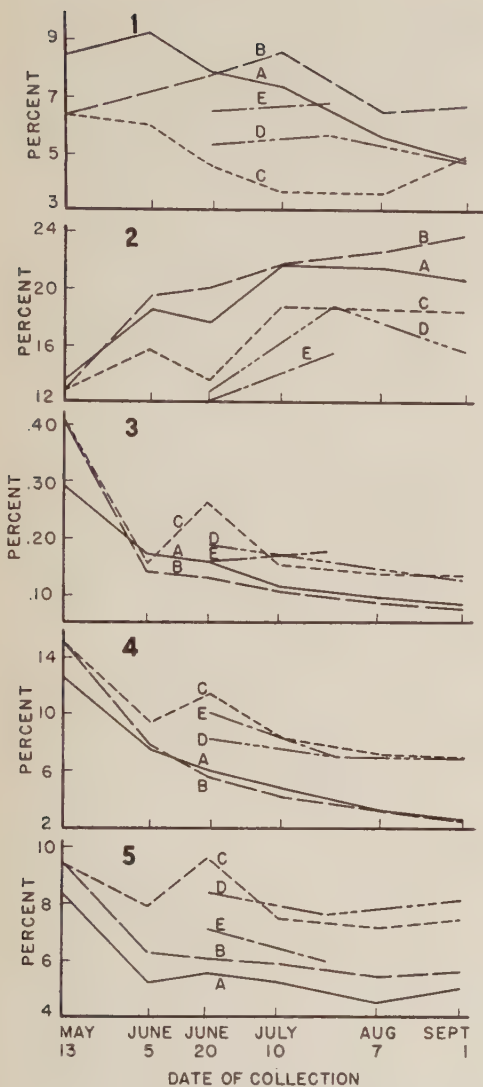


FIG. 1.—Total percentages (dry-weight basis) of (1) sugars and starch, (2) hemicelluloses, (3) soluble nitrogen, (4) "true" protein, and (5) ash in big bluestem at several stages of growth, clipped and not clipped. *A*, established plants on the upland; *B*, same on the lowland; *C*, same clipped plants on the lowland; *D*, clipped lowland seedlings; and *E*, clipped upland seedlings.

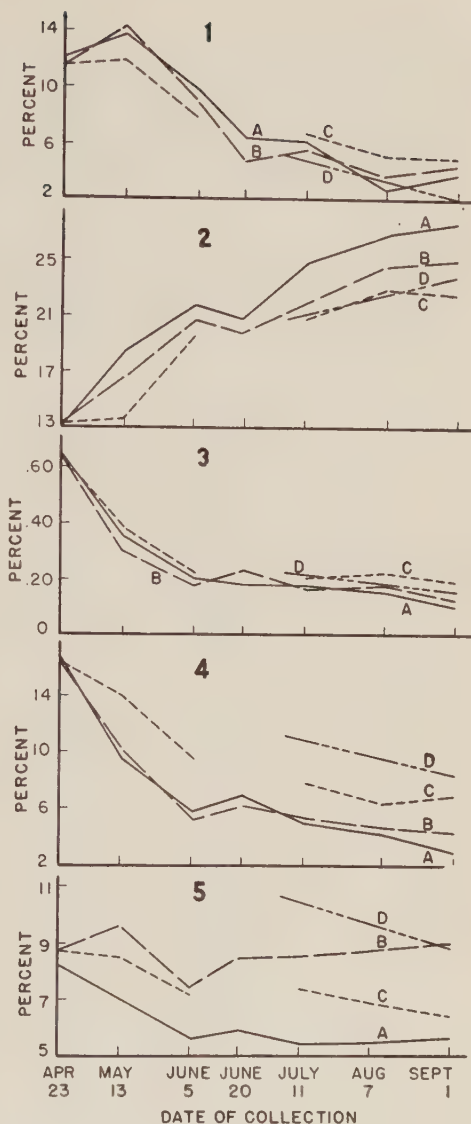


FIG. 2.—Total percentages (dry-weight basis) of (1) sugars and starch, (2) hemicelluloses, (3) soluble nitrogen, (4) "true" protein, and (5) ash in needle grass at several stages of growth, clipped and not clipped. *A*, established plants on the upland; *B*, same on the lowland; *C*, same clipped plants on the lowland; and *D*, clipped lowland seedlings.

usually had the highest percentage ash content.

The chemical composition of flower stalks and leaves of plants on the upland and on the lowland at the sampling on June 5 is shown in table 4. Flower stalks

plants shortly after the early leaf stage, the further slight decrease as the season advanced, and the gradual increase of the hemicellulose fraction throughout the growth cycle are in agreement with the results of other investigators (4, 8).

TABLE 4

PARTIAL CHEMICAL ANALYSIS OF ABOVE-GROUND PARTS OF NEEDLE GRASS AT SEVEN STAGES OF DEVELOPMENT, EXPRESSED AS PERCENTAGES OF OVEN-DRY WEIGHT

Plants	Date collected	Total sugars	Starch	Total sugars and starch	Hemi-cellulose	Soluble nitrogen	"True" protein	Total ash
Upland.....	April 23	6.3	5.7	12.0	13.1	0.65	16.8	8.3
	May 13	7.5	6.1	13.6	18.3	.35	9.6	7.0
	June 5	4.9	4.9	9.8	21.5	.20	5.7	5.6
	June 5*	5.4	5.6	11.0	21.2	.18	4.4	5.4
	June 5†	3.6	2.8	6.4	21.9	.24	8.8	6.0
	June 20	2.4	4.0	6.4	20.8	.19	6.9	5.9
	July 11	3.7	2.5	6.2	24.6	.18	5.1	5.4
	Aug. 7	0.8	1.8	2.6	26.7	.15	4.4	5.5
	Sept. 1	0.7	3.1	3.8	27.5	.10	2.9	5.6
Lowland.....	April 23	6.1	5.5	11.6	13.2	.64	16.6	8.8
	May 13	7.5	6.7	14.2	16.5	.30	10.1	9.6
	June 5	4.3	4.7	9.0	20.6	.18	5.3	7.3
	June 5*	4.5	5.0	9.5	20.5	.16	4.5	6.8
	June 5†	3.5	3.8	7.3	20.8	.22	7.7	8.8
	June 20	1.3	3.3	4.6	19.6	.23	6.2	8.5
	July 11	2.1	3.1	5.2	21.8	.17	5.5	8.5
	Aug. 7	0.5	3.5	4.0	24.5	.16	4.8	8.8
	Sept. 1	0.6	3.8	4.4	24.9	.12	4.4	9.0
Lowland, clipped....	April 23	6.1	5.5	11.6	13.2	.64	16.6	8.8
	May 13	6.5	5.3	11.8	13.7	.37	13.9	8.5
	June 5	3.3	4.4	7.7	19.6	.21	9.6	7.2
	July 11	2.5	4.0	6.5	20.9	.20	7.9	7.3
	Aug. 7	1.7	3.3	5.0	22.8	.22	6.4	6.9
	Sept. 1	0.7	4.0	4.7	22.6	.18	7.0	6.4
Upland seedlings....	June 20	0.9	7.8	8.7	16.2	.25	13.0	9.3
Lowland seedlings....	July 3	1.3	3.9	5.2	20.9	.22	11.3	10.7
	Sept. 1	0.6	1.4	2.0	23.8	0.15	8.5	8.9

* Analysis of stems and flowers.

† Analysis of leaves.

had a higher percentage content of sugar-starch but lower percentages of hemicellulose, soluble nitrogen, "true" protein, and total ash than did the leaves.

Discussion

The rapid percentage decrease of crude protein in established, unclipped

Early in the season unclipped established big bluestem on the upland usually had a higher percentage content of sugar plus starch than did big bluestem on the lowland. After June 20, however, when drought became severe on the upland, the situation was reversed. When soil moisture became depleted on the upland,

the tips of the leaves of big bluestem began to die back and dry up, resulting in decreased photosynthetic activity. The degree of development of established unclipped needle grass on the upland and the lowland was quite similar throughout the season of growth. On June 11, however, leaves of needle grass on the upland were rolled tightly because of drought, and, later, more drying of foliage occurred on the upland than on the lowland. This may partially account for the lower sugar-starch percentage in needle grass on the upland at the last two times of sampling.

It has been shown that part of the change in composition of forage with advancing maturity is the result of leaching of soluble constituents (9). The sugar fraction could be readily leached from the dried grass leaves. Although precipitation was abnormally low during the latter part of the growing season, the rains on June 27 and August 23 of 1.00 and 0.49 inches, respectively, may have caused considerable leaching. Since much drying-out of leaves occurred in the unclipped established plants on the upland and less drying occurred on the lowland, more leaching would be expected from the former plants.

It was noted that early in the season when the percentage of starch in big bluestem was high, the percentage of sugar was low, but that, as the season progressed, the situation was reversed. Perhaps a partial explanation for this is that these fractions are closely interrelated. Investigations with frequent samplings, however, are necessary for proof that these are seasonal changes and not those of daily or short duration.

In reviewing the literature, EATON (6) noted that opinions are still in conflict as to whether acid-hydrolyzable carbohydrates (hemicellulose) are used in

metabolism or whether they are permanent structural constituents of the cell wall. McCARTY (14, 15), in experiments with the wild oat (*Avena fatua*) and mountain brome (*Bromus carinatus*), found indications that the acid-hydrolyzable hemicellulose is largely employed as a structural material even by clipped plants. The percentage of hemicellulose in the unclipped big bluestem and needle grass generally increased during the advancing season, which suggests that this fraction is not used, at least in large amounts, as a reserve food. The percentage of hemicellulose in established upland big bluestem decreased slightly during the interval from June 5 to June 20. Big bluestem on the upland grew rapidly during this period, growing 6 inches in average foliage height. This rapid growth may have resulted in the addition of much succulent tissue, with a lower percentage of hemicellulose. The usually greater hemicellulose percentage in big bluestem on the lowland than on the upland may be due to the more stemmy nature of the former plants. Stems of big bluestem contain a slightly larger proportion of hemicellulose than do the leaves.

In established unclipped plants the proportion of available carbohydrates to available nitrogenous compounds progressively increased with the stage of development of the plant. These data are in agreement with the findings of KRAUS and KRAYBILL (10), who showed that when plants were vigorously vegetative but unfruitful, the proportion of available carbohydrates to nitrogen was relatively low, but in plants which were vigorous and also reproductive the relative proportion of these was intermediate.

The clippings from seedlings clipped several times during the growing season were in a succulent condition. This was reflected in the high percentages of sol-

uble nitrogen, "true" protein, and low percentage of hemicellulose. Foliage which grows after clipping or grazing is approximately as succulent as is that in the spring.

Clippings from the established plants which were periodically clipped on the lowland were also succulent and showed high percentages of soluble nitrogen and "true" protein and a low percentage of hemicellulose at the times of sampling. The rapid decrease in the percentage of the sugar-starch fraction in the clipped grasses during their development probably resulted from the rapid conversion of the products of photosynthesis into structural materials. MCCARTY (14) reported that in the wild oat there was low food (sugar and starch) concentration in the herbage regenerated after cutting. He showed in mountain brome in California that the annual herbage growth and yield are products of carbohydrates manufactured currently in the herbage (15). The carbohydrates in the roots and stem bases of mountain brome were at a minimum shortly after snow disappeared in spring.

The results from clipped big bluestem and needle grass indicate that the chemical composition varies during the season, even though the herbage is maintained in a succulent condition by repeated clipping. ARCHIBOLD and NELSON (1) have stated: "Grass kept in the vegetative stage by grazing may be quite different in chemical composition in midsummer from what it was in the spring. The seasonal factors, rainfall, temperature, sunshine, and length of day, exert their influence irrespective of the stage of growth of the plant."

Since the total soluble nitrogen, "true" protein, and total ash percentages were higher in grasses remaining in the leaf stage than in plants that had developed

flower stalks, it is probable that the former plants are more nutritious forage for animals. CLARKE and TISDALE (4) found that, in junegrass (*Koeleria cristata*), common speargrass (*S. comata*), and grama grass (*Bouteloua gracilis*), leafage was generally richer in crude protein, total ash, calcium, and phosphorus, and lower in percentage of crude fiber than the culms.

An explanation of the causes for the difference in chemical composition of established plants on the upland and the lowland is difficult, because possible differences in several factors of the environment—water content of soil, humidity, light, temperature, soil solutes, and soil air—may have directly affected the plants. The chemical composition of plants is closely associated with their stage of growth. In this experiment the stages of growth of big bluestem varied greatly between plants on the upland and on the lowland; only on the lowland did flowering occur. The differences in degree of development of needle grass in the two habitats was slight, but more drying of foliage occurred in plants on the upland. Since the supply of available water was probably the most critically controlling environmental factor in determining the degree of development and drying of the plants, varying water content between upland and lowland was perhaps the primary factor associated with the chemical differences between the plants.

The variation in height and density of stand of big bluestem on the upland, as contrasted with its growth on the lowland, may have been of importance in the chemical differences. In the taller and denser stand on the lowland the lower leaves would be shaded, with corresponding limitations on their rate of photosynthesis. This might bring about variation

in the entire chemical composition of the plant.

The scattered plants of big bluestem on the upland might be genetically different from plants on the lowland. Big bluestem grows normally in low moist soil, and the plants which persisted on the dry hill-crests might be a drought-resistant strain. The scattered bunches of needle grass on the lowland might, on the other hand, be a strain adapted to a moist environment. If this were true, the same species in the two habitats might have differing chemical composition even if grown under identical conditions. The use of identical clones in each area would eliminate this possibility for error.

It is generally agreed that frequent clipping of tops of plants usually reduces the yield both of tops and of roots. In eastern Nebraska, BISWELL and WEAVER (2) found that the dry weight of tops from sods of big bluestem clipped seven times during the season of growth was only 14.5 per cent of that of unclipped plants and that the dry weight of roots from clipped plants was only 5.3 per cent of that of controls. The low percentage content of the sugar-starch fraction usually present in the clipped big bluestem and needle grass was probably associated with a decreased production of tops and roots.

These data may be of significance in estimating the value of forage plants growing in different habitats. For example, if the chemical composition of big bluestem or needle grass growing on the upland and lowland is known, one should be able to estimate their relative forage values when the analytical data are used in conjunction with the yields and palatability of the grasses in the two habitats. Digestion trials should be used in conjunction with analytical data, as it has been shown that chemical analysis when

used alone may sometimes be misleading. Forages of similar composition may have different digestibilities and thus be of unequal value to the animal (16).

A knowledge of chemical composition of clippings from cut forage is important in comparing seasonal value of the clippings with that of plants allowed to grow to maturity. A study of chemical composition would be a valuable adjunct to all experiments in which the reaction of forage to clipping or grazing is studied.

Summary

1. The seasonal trend of certain chemical constituents of established big bluestem (*A. furcatus*) and needle grass (*S. spartea*) growing on lowland and upland habitats in eastern Nebraska was studied. The effects of periodic clipping on the composition of established and seedling plants were also investigated.

2. The growing season was characterized by a late spring; sufficient rainfall in April, May, and June; and severe drought in July and August. Mean monthly temperatures were all above normal. After late June little soil moisture available for growth occurred on the upland. On the lowland, water remained available, at least in small amounts, throughout the investigation.

3. Established big bluestem plants on the lowland became taller than those on the upland. The latter showed severe drought effects early in July, and flowering occurred only in the lowland plants. The degree of development of needle grass in the two habitats was similar, although more drying of foliage occurred in plants on the upland. During the flowering stage, grasses with flower stalks and grasses remaining in the leaf stage were separately collected.

Established grasses on the lowland regenerated after five cuttings. Seeds plant-

ed on the upland and lowland produced seedlings, which were clipped from one to three times.

4. The sugar plus starch percentage was greater in big bluestem on the upland than on the lowland early in the season, but later the situation was reversed. The percentage decreased in big bluestem on the upland when the leaves began to dry up. This drying may have reduced photosynthesis and may have permitted the soluble sugars to be leached from the leaves.

The hemicellulose percentage in big bluestem was usually higher in established plants on the lowland, perhaps because of their more stemmy nature. Needle grass on the upland, however, had a higher percentage of hemicellulose than lowland plants. Indications were that hemicellulose is not used as a reserve food.

5. Varying available water content between the upland and the lowland was probably the primary factor in causing the established unclipped plants in the two habitats to be chemically different,

since the supply of available water was probably the most critically controlling factor in determining the degree of development and drying of the plants.

6. Clippings from established plants which were periodically clipped were succulent, and their percentages of soluble nitrogen and "true" protein were high, but their percentage content of hemicellulose was low. Clippings from seedlings showed generally similar results.

7. The soluble nitrogen, "true" protein, and total ash percentages were higher in grass remaining in the leaf stage than in plants with flower stalks, but the sugar-starch percentage was greater in the culms.

8. This investigation may be of value in comparing the forage value of big bluestem and needle grass in different habitats and under grazing.

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